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GLACIATED PRAIRIE WETLAND FUNCTIONS AND VALUES: A SYNTHESIS OF THE LITERATURE

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GLACIATED PRAIRIE WETLAND FUNCTIONS AND VALUES: A SYNTHESIS OF THE LITERATURE

by

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SUMMARY

Prairie pothole wetlands are focal points in the hydrologic regime of the prairies. They store runoff water, thereby serving as potential floodwater storage reservoirs, and allow it to evapotranspire to the atmosphere or slowly seep into the groundwater. Leaving prairie pothole watersheds intact (i.e., not artificially draining them) will not prevent flooding in lower portions of the watersheds. However, artificially draining these watersheds may make flooding problems worse. Potholes can be either groundwater recharge sites, discharge sites, or groundwater flowthrough systems, and can temporarily change from one type to another depending on fluctuations in the watertable. The distribution of salts and degree of soil development indicate the long-term average direction of water movement between wetlands and groundwater. Recharge to the groundwater in the surficial glacial deposits of the area is important to the maintenance of high water tables. High watertables provide water for livestock via dugouts and may be vitally important to the long-term water balance of the prairies by providing significant recharge to soil moisture. The artificial drainage of groundwater flowthrough or discharge wetlands may lead to soil salination problems. Along with water, nutrients and sediments are detained, or trapped, in potholes. Valuations of the hydrological and nutrient/sediment entrapment functions of prairie potholes have not been done.

The emergent wetland plants found in temporary and seasonal wetlands can provide abundant forage for livestock. Forage quality is variable depending on species and time of use. The value of wetland forage would be the same as comparable upland forage on a weight basis. However, yields are much higher in these wetlands than on native upland sites, or for domesticated or introduced cool-season grasses.

Wildlife support is the best known function of prairie wetlands, especially in terms of waterfowl. These wetlands are critical to the maintenance of waterfowl populations on the continent. They also provide habitat for furbearers, resident game species, and many species of non-game wildlife. Direct valuation of the wildlife supported by these wetlands has not been undertaken. However, the value of the hunting recreation supported by wetland wildlife, fur harvest, and live bait production is substantial.

The expression of hydrologic and wildlife support functions is greatest when whole wetland complexes remain intact. It is the abundance of wetland basins distributed over the landscape that provides the most productive waterfowl breeding habitat, the most effective runoff water retention, and the best distribution of groundwater recharge.

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INTRODUCTION

The Prairie Pothole Region (PPR) is an area of glaciated landscapes in north-central North America. The PPR extends from north-central Iowa and western Minnesota, through those parts of the Dakotas east and north of the Missouri River, across the northern portion of Montana, and well into the provinces of Manitoba, Saskatchewan, and Alberta (Figure 1). The numerous depressions (termed "potholes" by biologists) left behind by the glaciers periodically fill with water, forming wetlands primarily of the Palustrine System with varying water-regimes (classified according to Cowardin et al. 1979). The PPR is the single most important area for breeding waterfowl, especially dabbling ducks (*Anas* spp.), on the North American continent (Smith et al. 1964; Crissey 1969; Bellrose 1979).

Many of the wetlands in the PPR have been drained for agricultural production (Frayer et al. 1983; Tiner 1984). Over 95% of the natural wetlands in Iowa have been drained (Bishop 1981), and it has been estimated that about 53%, 35%, and 60% of the wetland area in Minnesota, South Dakota, and North Dakota, respectively, has been drained (Tiner 1984). While most of the drainage has been by private landowners, much of it has been facilitated by various ,Federal Government projects and programs (Bonnema and Zschomler 1974; Erickson et al. 1979; Heimlich and Langner 1986; Nomsen et al. 1986).

In recent years, wetland losses due to many Federal Government activities require mitigation. Wetland mitigation may take the form of restoring drained wetlands, creating new wetlands, or enhancing existing wetlands. In order to fully evaluate the functions and values of prairie pothole wetlands that are drained or impacted by Federal projects and programs, and to adequately plan for their mitigation, a thorough review and synthesis of the literature is needed by biologists charged with the preparation of environmental assessments, impact statements, and mitigation plans. Major reviews of wetland functions and values exist for the nation as a whole (e.g., Greeson et al. 1979; Sather and Smith 1984), but provide little practical assistance to field biologists in the PPR. A number of good reviews and bibliographies exist for prairie wetland functions and values that include information on the floral, faunal, hydrologic, pedologic, and general ecologic functions and socio-economic values of prairie wetlands (Hubbard 1981; Leitch 1981a,b; Leitch and Saxowsky 1981; Ogaard 1981a,b,c; Linder and Hubbard 1982; Fulton et al. 1986; Berry et al. 1987). However, despite this plethora of publications on prairie wetland functions and values, the somewhat disjunct nature of the information in these publications makes it difficult for a field biologist to synthesize and apply this knowledge to specific wetlands and wetland complexes. In addition, some important works were overlooked by these reviews and some new information has become available since their publication. The purpose of this report is to incorporate the information

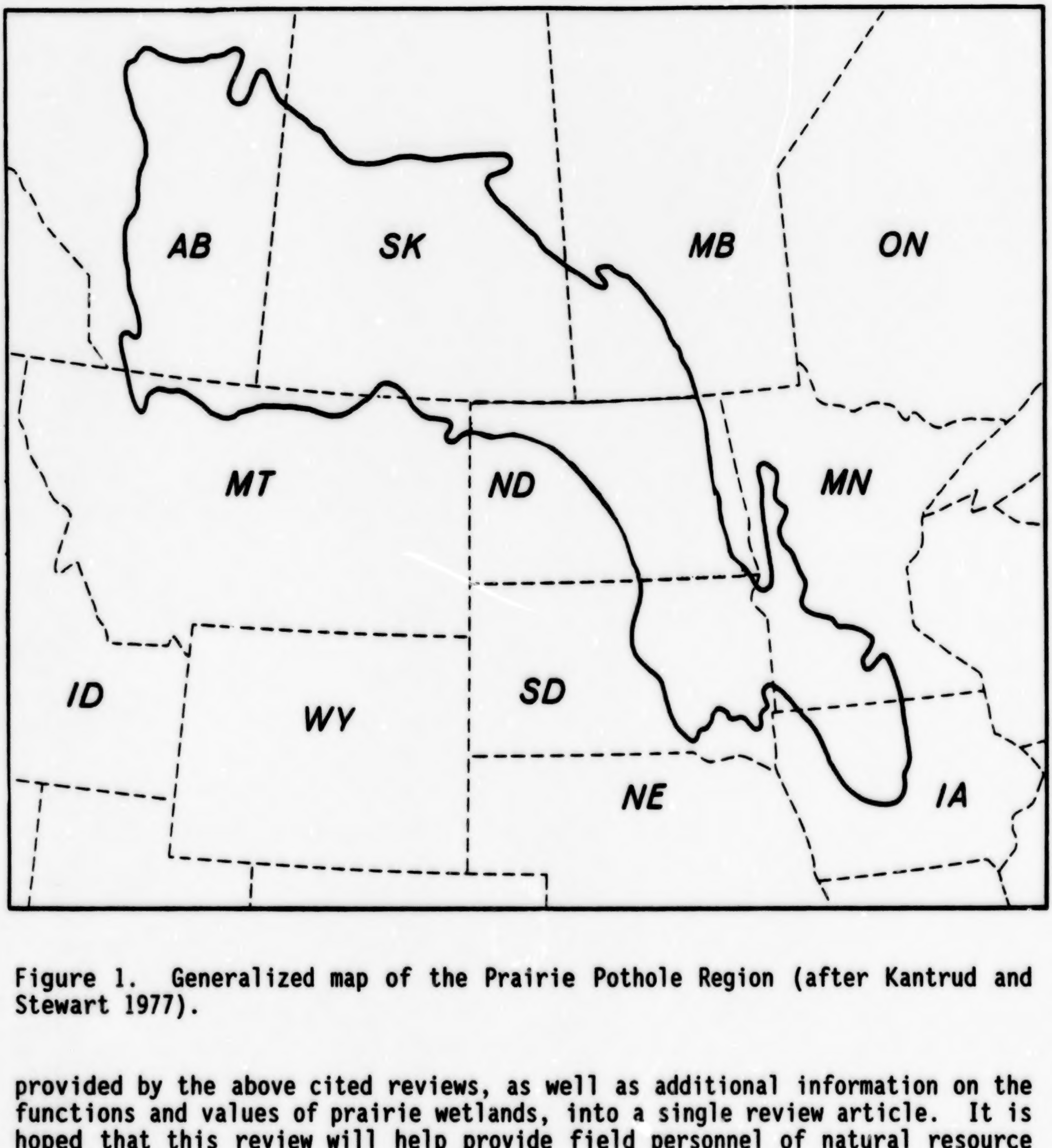

Figure 1. Generalized map of the Prairie Pothole Region (after Kantrud and Stewart 1977).

provided by the above cited reviews, as well as additional information on the functions and values of prairie wetlands, into a single review article. It is hoped that this review will help provide field personnel of natural resource agencies with the information needed to begin to address the difficult task of adequately assessing the functions of wetlands on a case-by-case basis.

In this report, "function" refers to the role that these wetlands play in the support of prairie biota and hydrology while "value" refers to the economic (i.e., monetary) value of these functions. The literature on the ecological functions of prairie wetlands is much more extensive than the literature on their values. Hence, the emphasis in this report on wetland functions is not by design, but by default. As the various functions of prairie wetlands are discussed, the value of the functions will be presented if known. Although there is a growing body of literature on methods for assessment of wetland functional values, it is not the intent of this review to include a comprehensive review of this topic.

CLASSIFICATION OF PRAIRIE WETLANDS

A thorough understanding of the systems used to classify prairie wetlands is necessary because assessment of some functions can be facilitated by proper classification.

NATURAL DEPRESSIONAL WETLANDS

Four classification systems have been used for glaciated prairie wetlands. The oldest is that of Martin et al. (1953). This system was printed in an abridged form by Shaw and Fredine (1956) (a more widely available publication) and is commonly referred to as the "Circular 39 system"--the number of that publication. This system has been in widespread use by field personnel of the U.S. Fish and Wildlife Service (FWS) and U.S. Soil Conservation Service (SCS) as well as other Federal agencies, and is still being used because of its reference in certain Federal and State acts and statutes.

The Circular 39 system is a very general system and frequently classifies wetlands that are dissimilar in many respects into the same "Types" (Table 1). The primary reason for this is the system's heavy reliance upon water depth as a classification criterion. In development of regional classification systems that would better describe glaciated prairie wetlands, Stewart and Kantrud (1971), in the U.S., and Millar (1976), in Canada, recognized that water permanence (i.e., duration of ponding or flooding), as modified by water chemistry (i.e., salinity), are much better classification criteria than depth. Both of these regional systems are similar in many respects. However, in order to keep the discussions that follow from being too awkward, and due to the more widespread use of the Stewart and Kantrud system in the literature, the system of Millar will not be reviewed here. Readers that may prefer the Canadian system are referred to Millar (1976: Tables 1 and 4, and Figure 5) for cross-referencing with the Stewart and Kantrud system.

The Stewart and Kantrud (1971) system classifies depressional prairie wetlands into seven classes (Table 1). These classes are defined by the wetland zones present in the deepest part of the depression, as long as it constitutes greater than 5% of the surface area of the entire wetland. Wetland zones are defined by the plant species present and are a reflection of the water regime (i.e., duration of ponding). The wetland-low-prairie zone is inundated for only a few days at a time and typically only in the very early spring, immediately after snow-melt. If this zone is the only wetland zone present, then the wetland is classified as a Class I, or ephemeral pond. The wet-meadow zone reflects a duration of ponding that averages from about one to a few weeks. If this zone is present in the deepest part of the depression, then the wetland is identified as a Class II, or temporary pond. A Class III wetland, or seasonal pond,

Table 1. Comparison of 3 systems used to classify depressional glaciated prairie wetlands.[a]

Stewart and Kantrud (1971)		Cowardin et al. (1979)	Martin et al. (1953)
Class	Zones[b]	Water regime modifier[d]	Type
I-Ephemeral ponds	Wetland-low-prairie	—[e]	1
II-Temporary ponds	Wet-meadow	Temporarily flooded	1,2
	Wetland-low-prairie	—	
III-Seasonal ponds	Shallow-marsh	Seasonally flooded	3,4
	Wet-meadow	Temporarily flooded	
	Wetland-low-prairie	—	
IV-Semi-permanent ponds	Deep-marsh	Semi-permanently flooded[f]	3,4,5,10,11
	Shallow-marsh	Seasonally flooded	
	Wet-meadow	Temporarily flooded	
	Wetland-low-prairie	—	
	Fen[c]	Saturated	
V-Permanent ponds and lakes	Permanent-open-water	Permanently flooded	5,11
	Deep-marsh	Semi-permanently flooded[f]	
	Shallow-marsh	Seasonally flooded	
	Wet-meadow	Temporarily flooded	
	Wetland-low-prairie	—	
	Fen[c]	Saturated	
VI-Alkali ponds and lakes	Intermittent alkali	Intermittently flooded[g]	9
	Shallow-marsh	Seasonally flooded	
	Wet-meadow	Temporarily flooded	
	Wetland-low-prairie	—	
	Fen[c]	Saturated	
VII-Fen ponds	Fen	Saturated	8
	Wet-meadow	Temporarily flooded	
	Wetland-low-prairie	—	

[a] Compiled from tables presented in Stewart and Kantrud (1971) and Cowardin et al. (1979).

[b] Zones are listed from top to bottom, within each Class, from the central zone to the outermost peripheral zone.

[c] Fen zone occurs as marginal pockets.

[d] Most glaciated prairie depressional wetlands are in the Palustrine System in this system. However, some can be in the Lacustrine system (see text). Predominant Classes are Emergent Wetland, Aquatic Bed, and Unconsolidated Bottom (see text).

[e] The wetland-low-prairie zone of Stewart and Kantrud (1971) is not considered wetland according to Cowardin et al. (1979).

[f] The deep marsh zone of Stewart and Kantrud (1971) also includes wetlands with a water regime of "intermittently exposed".

[g] With water chemistry modifier of "saline" or "hypersaline".

contains a shallow-marsh zone in the deepest part and reflects a ponding duration that averages longer than that of a wet-meadow zone, but is not ponded for the entire growing season. The presence of a deep-marsh zone indicates that ponded water typically lasts for the majority of the growing season. Depressions containing a deep-marsh zone are Class IV, or semi-permanent ponds. Class V wetlands, or permanent ponds, contain a permanent-open-water zone and are commonly referred to as lakes. Class VI wetlands, or alkali ponds, contain an intermittent alkali zone of very high electrical conductivities. Class VII wetlands, or fen ponds, contain a fen zone and are typically also high in electrical conductivity and, although they may occasionally have surface water present, are usually saturated to the soil surface due to a stable watertable. The means by which to classify wetlands in the Stewart and Kantrud system is the species composition of the vegetation. Species lists for the wetland classes and zones for the various salinity subclasses are provided in Stewart and Kantrud (1971).

A zonation pattern of more-or-less concentric bands of wetland zones around a central zone is typical of prairie potholes (Stewart and Kantrud 1971) (see Table 1). This is especially true of Classes II, III, and IV, which are the most common types of wetlands in the Dakotas (Stewart and Kantrud 1973; Ruwaldt et al. 1979) and probably the rest of the PPR as well. These zones typically grade from the "most permanent" in the center outwards to the "least permanent." But frequently zones are patchy or missing, or even reversed in order, due to abrupt changes in water level. Fen zones are frequently found in small patches around the periphery of Class IV and V wetlands. Within each class of wetlands, the Stewart and Kantrud System also classifies subclasses of each that correspond to salinity categories. The subclasses are based on average electrical conductivities of the pond water as reflected by the dominant vegetation. A single-point-in-time measurement of conductivity, however, may not always be reliable in classifying to subclass, as a recent runoff event may dilute the salts or they may be concentrated due to drawdown. Additionally, cover types can be assigned to each pothole. These cover types describe the degree of interspersion of emergent plant cover and open water, which can be quite variable between years (Weller and Spatcher 1965; Stewart and Kantrud 1971; Millar 1973, 1976).

The Cowardin et al. (1979) system was designed to be used across the entire country and to replace the Circular 39 system. Lists of wetland indicator plant species (Reed 1986) and hydric soils (U.S. Soil Conservation Service 1985) have been devised to augment this system. The Cowardin system does a much better job of classifying various kinds of wetlands than Circular 39 did, and is the system currently being used by the FWS in conducting the National Wetland Inventory. The Cowardin system will be used in the present report. The major classifaetory level of the Cowardin system is termed "System." All depressional wetlands in the glaciated prairie region are in the Palustrine System, with the exception of those wetlands lacking emergent vegetation and those that are over 8 ha or greater than 2 m deep at low water. These latter large or deep openwater wetlands are in the Lacustrine System. The next level in the hierarchy of the Palustrine System is the Class, of which most pothole wetlands are likely to be in the Emergent Wetland, Aquatic Bed, or Unconsolidated Bottom Classes. The Class level in the Cowardin system is similar, at least in prairie potholes, to the cover type of the Stewart and Kantrud system, in that it can vary from year to year at the same site due to hydrologic or herbivore activity, or other perturbations of the site (Weller and Spatcher 1965; Stewart and Kantrud 1971; Millar 1973, 1976).

Although there are other levels of classification in the Cowardin system hierarchy that can be useful in classifying prairie pothole wetlands, the use of "water regime modifiers" is perhaps the most discriminatory. The water regime modifiers that correspond to the wetland zones of Stewart and Kantrud are listed in Table 1. A translation between the two systems is fairly easy to make. The major difference between the two systems is that the Stewart and Kantrud system classes wetlands at the highest level based on a physiognomic concept. The Cowardin system, rather, is entirely an area based concept. To illustrate this, a Class IV wetland by the Stewart and Kantrud system may contain three wetlands by the Cowardin system (Classes omitted): a palustrine semipermanently flooded wetland, a palustrine seasonally flooded wetland, and a palustrine temporarily flooded wetland. A more detailed comparison of the two systems has been made by Cowardin (1982). The use of the Cowardin system to describe a prairie pothole wetland is very discrete and exact (as the above example demonstrates), but can be rather cumbersome when discussing an individual prairie pothole. In much the same manner that the Stewart and Kantrud system uses the "wettest" zone to classify a basin, the discussions in this report will classify basins using the Cowardin system but by naming only the "most permanent" water regime present. Descriptions of water regimes will be abbreviated. For example: temporarily flooded, seasonally flooded, and semipermanently flooded will be abbreviated to temporary, seasonal, and semipermanent. These conventions will greatly reduce the number of words needed to describe a pothole. A Class IV wetland will be termed a "semipermanent-wetland-dominated" basin or pothole. A Class III wetland will be termed a "seasonal-wetland-dominated" basin, and a Class II wetland will be termed a "temporary-wetland-dominated" basin.

OTHER WETLANDS

The other types of wetlands in the glaciated prairie region are primarily nondepressional (i.e., rivers and streams) or manmade (e.g., impoundments or excavated). These other types of wetlands compose only a small percentage of the wetland area in the PPR of the Dakotas. Stewart and Kantrud (1973) estimated that natural basin wetlands composed 93% of the water/wetland surface area in the PPR of North Dakota. The remaining 7% consisted of all other water bodies (e.g., streams, oxbows, stockponds, dugouts, reservoirs, ditches, sewage lagoons). In South Dakota, Ruwaldt et al. (1979) estimated that natural basin wetlands composed 90% of the water/wetland area in that State's portion of the PPR.

Perennial rivers and streams in this region are classified in the Riverine System and Lower Perennial Subsystem according to Cowardin et al. (1979). Intermittent streams in this region usually flow for only a few weeks or months and fill-in across the entire channel with emergent hydrophytes after cessation of flow. Due to the presence of emergent hydrophytes, intermittent streams are typically classified as Palustrine in the Cowardin system. Hubbard (1979) described several intermittent streams on the Souris Lake Plain in north-central North Dakota as consisting of a long series of intergradations between seasonal and semipermanent wetland with frequent patches of saturated (fen) wetland. The dominant plant species present in intermittent prairie streams are the same as those found in depressional wetlands; therefore, the water regime modifiers of Cowardin et al. (1979) or the wetland zones of Stewart and Kantrud (1971) can be applied to these streams. Man-made wetlands can typically be classified as Palustrine or Lacustrine in the Cowardin system, with appropriate water regime or other modifiers, or by the Stewart and Kantrud system, if an appropriate adjective is used to designate their anthropogenic origin.

HYDROLOGY AND SOILS

The hydrology of wetlands is the overriding cause of the expression of the characteristics of a given wetland. Where surface water and/or groundwater flow patterns cause water to stay near or above the soil surface for a significant period of time during the growing season, a wetland will occur. Various hydrologic "functions" have been ascribed to wetlands such as groundwater recharge or discharge and natural flood-water storage reservoirs (Carter et al. 1979; Sather and Smith 1984). These functions vary among individual wetlands within a locality or among groups of wetlands in different localities. In the discussion that follows, the hydrology of individual prairie wetlands will be reviewed first, followed by a discussion of the functions that wetlands may perform in the regional hydrology. Prairie pothole soils will also be reviewed in this section, as soils appear to be an excellent means by which to "read" certain hydrologic functions.

HYDROLOGY OF INDIVIDUAL WETLANDS

Glaciated depressional prairie wetlands receive their water from direct precipitation, meltwater from accumulated (drifted) snow, runoff from surrounding uplands, groundwater discharge, or a combination of several sources (Shjeflo 1968; Sloan 1970; Eisenlohr and others [sic] 1972). Water leaves a prairie pothole by one or more of the following ways: direct evapotranspiration from the pond, marginal evapotranspiration from the pond edge, groundwater recharge, or by overflow out of the depression during high water levels (Meyboom 1966a; Shjeflo 1968; Sloan 1970; Millar 1971; Eisenlohr and others 1972). It is the relationship between the hydrologic inputs and outputs of each pothole that determines the water regimes found within it.

An important point to be remembered in these discussions is that throughout the PPR, average annual precipitation is always less than the average annual evaporation (Omodt et al. 1968; Millar 1969; Spuhler et al. 1971). Thus, evapotranspiration is a constant driving force during the growing season that pushes a wetland toward dryness. It is the amount of water entering a pothole from runoff, meltwater from drifted snow, or groundwater discharge that is in excess of direct precipitation that governs a pond's permanency.

Runoff into potholes occurs during the spring thaw when melting snow or precipitation flows over frozen soil, or during the frost-free season when precipitation rates exceed the infiltration capacity of the soil. The glacial-till-derived soils of the region are high in smectite clays, which expand greatly when wet and are the primary cause of low permeabilities of the soils. The amount of runoff that a pothole will receive can vary greatly between years and the relative contribution of snow-melt runoff and growing-season runoff can also vary greatly (Shjeflo 1968; Millar 1969). This is also true among localities in the same year. Variations in annual precipitation and temperature patterns and extremes are normal in the glaciated prairie region (Spuhler et al. 1961; Omodt et al. 1968).

Other than seepage to groundwater and basin overflow, the major route of water leaving a pothole wetland is by evapotranspiration (Shjeflo 1968; Allred et al. 1971; Millar 1971). Evapotranspiration can not only be separated into its components, evaporation and transpiration, but also it can be separated into that which occurs from the pond per se and that from the marginal plants and soil (Millar 1971). This marginal evapotranspiration is important in all pothole wetlands in terms of soil formation. However, in terms of water budgets, it is quantitatively most important to the smaller wetlands. Millar (1971) attributed from 60% to 80% of the water loss from ponds less than 0.4 ha to marginal evapotranspiration, but not more than 30% to 35% of total loss in ponds larger than 0.4 ha. In that study, the rate of water loss varied directly with the length of shoreline per unit of pond surface area, and although only ponds of about 4.0 ha or less were studied, it would only seem logical that as ponds become very large the effect of marginal evapotranspiration would become a very small part of total water loss. In regard to evapotranspiration from the pond, Shjeflo (1968) reported a 5-year May to October mean of 64.3 cm in 10 North Dakota potholes (all seasonal-wetland-dominated and semipermanent-wetland-dominated basins) of moderate to large pond size (ca. 3 to 16 ha). This number is in the same range of values given by Allred et al. (1971) for several ponds. Even though the effect of emergent hydrophytes on evapotranspiration rates is variable (Bernatowicz et al. 1976; Idso 1981), it was found that vegetated potholes in North Dakota lost less water via evapotranspiration during the growing season than did openwater potholes (Eisenlohr 1966; Shjeflo 1968). This effect is caused by the sheltering of the water surface by the senescent plants at both the beginning and end of the growing season.

There are three general types of pothole wetlands in regard to groundwater (Lissey 1971; Sloan 1972; Winter and Carr 1980): groundwater recharge wetlands, groundwater discharge wetlands, and flowthrough wetlands that both recharge and discharge groundwater at various locations within the pothole. Depending on fluctuations in the water table, however, a pothole may temporarily change from one type to another (Lissey 1971; Winter and Carr 1980). The degree to which groundwater discharge takes place in a pothole wetland is roughly related to its salinity and, therefore, its electrical conductivity (Rozkowski 1969; Sloan 1972). Those with the freshest of waters are recharge wetlands, and those with the most saline waters are discharge wetlands. Flowthrough wetlands, however, have intermediate salinities. The higher salinities in discharge wetlands are a result of evaporative concentration of salts, with no mechanism for their removal (i.e., no downward movement of water). Major ions responsible for the salinity differences are Mg^{2+}, Na^{+}, and SO_4^{2-} (Rozkowski 1969; Sloan 1972; Stewart and Kantrud 1972; Arndt and Richardson 1986).

Electrical conductivity measurements in pothole wetlands at a point in time are generally not reliable for determination of groundwater regimes for two reasons. First, salinity fluctuates seasonally tending to be lowest in spring and highest later in the season due to concentration of salts at low water levels. Additionally, large runoff events can dilute the pond water. Second, variations in chemical composition of the soils, till, and other glacial drift, as well as which type of flow system a wetland is interacting with, can affect the background conductivity of the groundwater. These factors can cause local differences in groundwater conductivities such that general levels in pond waters of a certain area may be higher or lower than those of another area.

Groundwater flow systems in the PPR can consist of the following: local flow--where groundwater moves between adjacent potholes; intermediate flow--where groundwater may move at deeper depths and discharge into potholes not adjacent to the recharge source but still in the local area; or regional flow--where groundwater moves deep into the till and interacts with wetlands in distant areas (Toth 1963; Lissey 1971; Winter and Carr 1980). The major systems interacting in regional topographic highs (e.g., the "knob and kettle" or "hummocky moraine" areas of dead ice moraine) are typically local and intermediate, while those in regional topographic lows (e.g., ground moraine) may receive groundwater from regional flow systems that originate in adjacent hummocky moraine (Meyboom 1966b; VanVoast and Novitzki 1968). Within any given area, the factors influencing which system a wetland is interacting with depend on the topographic setting, position of the water table, thickness of the drift, anisotropy of the drift, and the configuration of the underlying bedrock (Freeze and Witherspoon 1967; VanVoast and Novitzki 1968; Winter and Carr 1980).

The classification of prairie pothole wetlands can roughly be related to groundwater relationships. Based on the information provided by Sloan (1962), Lissey (1968, 1971), Winter and Carr (1980), Richardson and Bigler (1984), Miller et al. (1985), Arndt and Richardson (1986), and Hubbard et al. (1988), it may be stated that (1) groundwater recharge wetlands are typically temporary-wetland-dominated and seasonal-wetland-dominated basins, (2) discharge wetlands are typically semipermanent-wetland-dominated, intermittently-exposed-wetland-dominated, permanent-wetland-dominated, saturated-wetland-dominated, and intermittently-flooded-(saline)-wetland-dominated basins, and (3) flowthrough wetlands are typically semipermanent-wetland-dominated basins. However, some seasonal-wetland-dominated, intermittently-exposed-wetland-dominated, and permanent-wetland-dominated basins may also be flowthrough potholes.

SOILS AS INDICATORS OF GROUNDWATER RELATIONSHIPS

On a Saskatchewan study area, Miller et al. (1985) found that in small recharge potholes, soils were nonsaline, noncarbonated (noncalcareous), had very deep sola (depth of soil development), and had well developed eluvial (highly leached) and argillic (clay enriched) horizons. All of these attributes indicate a consistent downward-moving water flow. In the U.S., soils of this type would be classified as Argialbolls (U.S. Soil Conservation Service 1975). Adjacent (i.e., immediately surrounding) to the Argialbolls is a zone of soil that is nonsaline but is calcareous. This calcareous soil is present due to the interception of water moving out of the depression due to transpiration by marginal plants, which causes the calcium carbonate to precipitate. This same phreatophytic phenomenon has been observed or implied by Meyboom (1966a), Millar (1971), and Malo (1975). These calcareous soils were nonsaline, as apparently enough water does move through these soils when temporarily ponded in the spring to leach out the salts before transpiration begins.

Miller et al. (1985) also found these same Argialbolls to occur in two larger recharge potholes, but they occurred not in the centers of the depressions but between a soil occupying the central portion and the calcareous ring. This central soil did not have the argillic horizon that the adjacent Argialbolls had, even though their groundwater flow measurements indicated recharge conditions. Miller et al. (1985) attributed the lack of an argillic horizon to the longer ponding duration of the soil. Argillic horizon development is facilitated by frequent wetting and drying cycles. Arndt and Richardson (1986) found a similar situation in a recharge wetland in North Dakota. In this case, a Typic Argiaquoll (soils similar to an Argialboll but without an eluvial horizon) was found surrounding a Cumulic Haplaquoll (a poorly developed Mollisol lacking an argillic horizon). Both soils were also nonsaline and noncalcareous.

In a groundwater discharge pothole, Miller et al. (1985) found that the soil was saline, calcareous to the surface, and had a well developed, shallow calcareous C horizon. These conditions indicate the upward movement of groundwater that brings with it dissolved salts causing the salinity and precipitation of calcite. In a North Dakota study, Arndt and Richardson (1986) found that soils in a discharge wetland (a semipermanent-wetland-dominated basin) were also calcareous and highly saline. These soils were classed as Mollic Fluvaquents in the peripheral temporary and seasonal wetlands and are very poorly developed soils. In addition, Arndt and Richardson (1986) studied a flowthrough wetland (also a semipermanent-wetland-dominated basin) and found that it contained Typic Calciaquolls in the peripheral temporary and seasonal wetlands, but while these soils were calcareous and salinelike in the discharge wetland, the electrical conductivities were less than half of those found at the discharge pothole. The recharge wetland (see above) studied by these authors was a seasonal-wetland-(fresh)-dominated basin, and both the discharge and flowthrough wetlands were semipermanent-wetland-dominated basins; the flowthrough wetland having a salinity in the oligosaline range and that of the discharge wetland was in the mesosaline to polysaline range (salinity modifiers according to Cowardin et al. 1979). These authors did not report soil classifications of the central semipermanent wetland in either of the semipermanent-wetland-dominated basins.

In another North Dakota study, Richardson and Bigler (1984) sampled the soils from all water regimes (and some dominance types within water regimes) of a semipermanent-wetland-dominated flowthrough wetland. They found Typic Haplaquolls under the peripheral temporary wetland and seasonal wetland, a Typic Fluvaquent under cattails (_Typha glauca_) in the semipermanent wetland, and Fluvaquentic Haplaquolls under bulrush (_Scirpus acuta_) and under the open water portion of the semipermanent wetland. All soils in all zones were calcareous and had similar electrical conductivities as the flowthrough wetland reported by Arndt and Richardson (1986).

Hubbard et al. (1988) conducted investigations of wetland soils in several prairie potholes in South Dakota. In two seasonal-wetland-dominated basins on the Altamont Moraine of the Prairie Coteau (see Flint 1955; Lemke et al. 1965), they found that the centers of the depressions were occupied by Typic Argiaquolls (Parnell series) (similar to the Argialbolls found by Miller et al. 1985, but lacking an eluvial horizon), surrounded by a calcareous ring of Typic Calciaquolls (Vallers series). The downslope edge of the Vallers polypedons occurred under the peripheral temporary wetland and extended upslope a few meters into the upland vegetation. Two temporary-wetland-dominated basins on the same study site also had Argiaquolls in the center (Parnell series) but had Typic Haplaquoll (Flom series) on the periphery. The Flom soils are not calcareous in the surface horizon like the Calciaquolls that encircled the seasonal-wetland-dominated basins studied. The water regime of a temporary-wetland-dominated basin probably does not allow for a groundwater mound to persist long enough to develop a calcareous "ring."

The central semipermanent wetlands in four semipermanent-wetland-dominated basins were also studied and found to have Cumulic Haplaquolls (Southam series). All four of these semipermanent-wetland-dominated basins are probably flowthrough sites based on the electrical conductivity of the waters (J. B. Millar, unpublished data). On two of the semipermanent-wetland-dominated basins, the edge soils were studied. These were Typic Calciaquolls (Vallers series) and they spanned from the peripheral temporary wetland into the upland.

Two seasonal-wetland-dominated basins in the James River Lowland situated on fairly thin end moraine (see Flint 1955) were also studied by Hubbard et al. (1988). These two wetlands had central soils of Typic Argiaquolls (Worthing series) with a patchy peripheral band of Argiaquic Argialbolls (Tetonka series). Both of these soils occurred entirely within the central seasonal wetland. In addition, small polypedons of a Typic Natraquoll (Hoven series) occurred on the periphery of these two seasonal-wetland-dominated basins. In one basin, the Hoven occurred in the seasonal wetland but with a species composition drastically different from the rest of the seasonal wetland due to the sodium in this soil series. However, the Hoven soil at the other pothole occurred, essentially, under upland vegetation.

Malterer et al. (1986) studied the soils of two large saturated wetlands (Denbigh Fen, 400 ha; Towner Fen, 100 ha) on the Souris River flood plain in North Dakota and found well-developed, calcareous, Histosols. These peat-forming environments are unusual in the prairie, but do occasionally occur. The constant saturation, due to the continuous high water table, prevents the oxidation of the organic matter and allows for its build-up. Although calcareous, these kinds of wetlands are not saline (Stewart and Kantrud 1972).

HYDROGEOLOGIC SETTING AND HYDROLOGICAL FUNCTIONAL SIGNIFICANCE OF PRAIRIE WETLANDS

Groundwater

The groundwater flow patterns in these glacial till landscapes are complex and dynamic (e.g., Winter and Carr 1980), but the important point is that prairie wetlands are all intimately associated with the groundwater systems. The true significance of these relationships can only be appreciated when it is realized that groundwater recharge only rarely occurs over the uplands and is "depression focused," i.e., it effectively occurs in wetlands where water is ponded (Freeze 1969; Freeze and Banner 1970; Lissey 1971).

Glacial till deposits are typically not aquifers by the hydrogeologists definition, in that an aquifer must be capable of yielding pumpable quantities of water (Davis and DeWiest 1966). However, glacial outwashes, occurring both as surficial deposits and buried within the till, are aquifers and are the source of water to on-farm wells in this region. Buried outwash obviously receives all of its water from the enveloping till. Surficial outwash deposits, being surrounded by till, may receive water from the till, but this has not been studied. In addition, water in the till is used directly by farmers for their livestock by use of "dug outs." Dug outs are small (0.1 ha) excavations intended to intercept the watertable. There are an estimated 56,000 dug outs in eastern South Dakota alone (McPhillips et al. 1983).

Since all pothole wetlands are associated with groundwater, the artificial drainage of wetlands may eventually lead to the effective preclusion of groundwater recharge and result in lowering of the watertable. This would lead to the drying-up of dug outs, the possible drying-up of surficial outwash aquifers, and a possible reduction in hydrostatic pressures in buried outwash aquifers or even their dewatering should the watertable drop low enough. No studies have been conducted to address these issues.

Aside from the use of prairie groundwater as water sources for livestock and humans, there is the possibility that a substantial amount of soil moisture recharge may be occurring from groundwater. It has been documented that when water tables are within about 2 meters from the bottom of the frozen soil zone (Willis et al. 1964), water can move upward from the water table to the frozen soil zone over the course of the winter in response to thermal gradients (Schneider 1961; Willis et al. 1964; Benz et al. 1968; Malo 1975). The data in Malo (1975), however, extends the depths to the water table over which this phenomenon can occur to about 4 m. Malo (1975) reported soil moisture increases due to this phenomenon of greater than 10% at the 60-cm depth at a summit position about 80 m from a recharge (seasonal-wetland-dominated basin) wetland in glacial till in North Dakota. The importance of this source of soil moisture recharge to agriculture across the glaciated prairies has yet to be assessed. It is noteworthy, however, that in a hydrologic modeling study of a central Iowa depressional watershed, the model consistently predicted higher soil moisture levels in the top 1.5 m of soil under corn within an undrained watershed versus a completely drained watershed (i.e., all potholes artificially drained) throughout the growing season (Campbell and Johnson 1975).

Groundwater recharge wetlands have some of the most highly developed soils of the prairies; sola are very deep, they are leached free of soluble salts and carbonates, and they have argillic horizons. If these soils are artificially drained, they can produce excellent yields of cultivated crops. However, the artificial drainage and cultivation of groundwater flowthrough or discharge wetlands can cause soil salination (Richardson 1986). The soils in discharge wetlands are saline to begin with, but those of flowthrough wetlands are only moderately saline at the surface. After artificial drainage and cultivation of a flowthrough wetland, groundwater is no longer transpired from depth in the soil by hydrophytes and is allowed to evaporate directly from the soil surface.

Therefore, salts that accumulated at depth are now free to accumulate at the soil surface. This same process can occur on the margins of flowthrough or discharge wetlands that are not artificially drained, but have their marginal Calciaquoll (or Natraquoll) soil in cultivation (Richardson 1986).

Surface Water

The effects that Palustrine wetlands that are adjacent to Riverine systems, have on flood attenuation is fairly well documented in the literature (see review in Sather and Smith 1984). However, in the PPR the relationship between wetlands, their artificial drainage, and flooding is still steeped in controversy. To appreciate the complexity of the situation, an understanding of the surface water hydrology of the area under natural conditions is necessary.

The depressional topography of the PPR presents an interesting problem to hydrologists. Under natural conditions the contributing drainage area of a stream, or terminal water body in a closed watershed, is not constant from year to year and can even vary seasonally. Stichling and Blackwell (1957) have described this phenomenon in detail. Following several years of below normal runoff, the depressions within the gross drainage area (gross drainage area is that plane area enclosed within its divide that would entirely contribute runoff to the main stream in extremely wet years) are empty, or nearly so, providing large amounts of storage. The net drainage area (that portion of the gross drainage area that will contribute runoff to the main stream in a particular year) under dry conditions can therefore be relatively small. Stichling and Blackwell (1957) measured a typical watershed in Canada and determined that the net drainage area under dry conditions for that particular basin was only 20% of the gross drainage area. Thus, during a major runoff event 80% of the gross drainage area would be noncontributing. After several years of above average runoff, the depressions would be full, or nearly so, and available storage would be low. The net drainage area under these conditions would approach the gross drainage area in size. A major runoff event that under dry antecedent depression conditions would yield little to the main stream, would contribute large amounts of runoff to the main stream under wet antecedent conditions.

Given the above scenario, it is logical to assume that as wetland depressions are drained, the net drainage area of a given watershed is permanently increased. As the net drainage area is permanently increased, the probability of a given runoff event producing flood levels in the receiving water body is, likewise, probably increased. The positive relationship between increasing drainage area and increasing discharge measurements has long been known to hydrologists (Strahler 1964).

Hydrological modeling studies by Campbell and Johnson (1975) in Iowa have predicted that artificial drainage via surface ditches can increase peak discharges in watersheds. Moore and Larson (1979) also used a hydrologic model calibrated on Minnesota data utilizing open pipe and tile drains. Their model predicted that artificial drainage of depressions increased annual runoff volumes significantly and, for individual storm events, increased peak flows for long duration, low intensity storms. Moore and Larson (1979) also used multiple regression to evaluate factors affecting mean annual floods in 73 watersheds in 4 States of the PPR. In their analysis two variables, area of the watershed and percent area in lakes and wetlands explained only 48% ($p<0.01$) of the variation in mean annual floods. However, when a subset of 23 watersheds from Minnesota only were used, the resultant equation explained 82% of the variation. The watershed area was positively associated with mean annual flood while percent of watershed in wetlands and lakes was negatively associated. In a modeling study of eight drainage projects in Saskatchewan, Dybvig and Hart (1977) found that the combined effects of the projects would cause an increase in flood peak on the Moose Jaw River of from 7% to 20% for a 10-year frequency flood and from 14% to 20% for a 20-year frequency flood.

If wetland drainage is having an effect on flooding, then it is reasonable to assume that floods should have increased as the number of drained wetlands have increased with time. Moore and Larson (1979) included in their discussion a cursory analysis of flows in the Minnesota River at Mankato. They divided the period of record for flows at Mankato into four equal time periods (19 years each) and calculated the mean annual flood values for each period. The mean annual flood for 1922-1940 was only 8,973 cfs (cubic feet per second), reflecting the drought of the 1930s. From 1903-1921 the mean annual flood was 21,381 cfs. From 1941-1959 the value was 21,108 cfs a 1.3% drop from the 1903-1921 average but very comparable. However, the mean annual flood from 1960-1978 was 24,871 cfs an 18% increase over the 1941-1959 mean. Moore and Larson (1979) were skeptical about whether or not this increase was caused by drainage development.

Kloet (1971) compared runoff from a relatively undrained watershed with that from a highly drained watershed in northeast North Dakota. Peak discharges for the year 1904-1941 were compared to those from 1942-1970 for the Pembina River at Neche, North Dakota. Those years in each time period with very high precipitation or low precipitation were deleted from the comparison. It was concluded that flood peaks after 1942 were "significantly higher" than those prior to 1942, while average precipitation was similar. The higher discharges since 1942 were attributed to either increased wetland drainage or changes in agricultural practices, or a combination of both.

Rannie (1980) studied the historic flows in the Red and Assiniboine Rivers in and upstream from Winnipeg, Manitoba. He found that the frequency of flood events has doubled on the Red River since 1950, as compared to the previous 58 years. From 1969 to 1979 the mean annual maximum discharges for the Red and Assiniboine Rivers were, respectively, more than 80% and 60% higher than the 1913-1968 average. From the beginning of the record to 1978, both rivers demonstrated a rising trend in maximum annual discharge. The author tentatively concluded that a combination of both hydro-meteorological factors and man-made factors, including the reduction of natural water storage due to agricultural drainage schemes, may be the cause.

Brun et al. (1981) studied historic stream flow changes at nine locations on four North Dakota tributaries of the Red River spanning 14 to 46 years. They regressed mean annual flows, maximum daily flows, and mean spring (March, April, May) flows on time. At nearly all locations the regression equations for all three parameters indicated that flows have increased over time with regression equations for locations farthest downstream usually being statistically significant. These researchers also regressed flows on mean annual precipitation and found that flows increased with precipitation; several equations were statistically significant. When precipitation was regressed on time, it was demonstrated that there had been no significant changes in precipitation over the same time periods that stream flows have increased. Thus, the increase in flows of the streams cannot be related to meteorological changes. These results prompted the authors to further investigate the situation on two of the four streams. The catchment basins of the two rivers were determined using U.S. Geological Survey maps and field surveys. It was found that because of artificial drainage, the current drainage basins are much larger than the original basins. Assuming that artificial drainage started at the time flow records began at several of the stream locations and has proceeded annually in a fairly uniform manner, the authors found that the increase in predicted flow rates is strongly related to the increase in drainage area (due to artificial drainage) in each basin.

The above cited studies have all provided strong evidence, especially when viewed in total, that wetland drainage can increase watershed discharges and has probably had an impact on flooding. These studies, however, have all been based on empirical statistics or simulation. Experimental studies have not been undertaken and probably never will; it is difficult to imagine experimental units the size of watersheds in the PPR. Not surprising, then, is the fact that no experimental studies have been conducted on the economic impacts of wetland drainage in terms of flooding effects. Ludden et al. (1983), however, have placed some importance on the water storage functions of wetlands in the 976,000-ha Devils Lake Basin in North Dakota. They found that small wetlands could contain 81,100 ha-m (657,000 acre-ft) of water--equivalent to about 72% of the total runoff volume from a 2-year frequency runoff and about 41% of the total runoff volume from a 100-year frequency runoff. These investigators could not valuate this storage function. The Devils Lake Basin Advisory Committee (1976), however, placed an estimate of $48.30 for the annual personal income generated in the Devils Lake Basin for each acre of restored wetland; they also estimated that each acre of restored wetland in the Basin would reduce flood damages to transportation facilities by $2.46.

Other studies that contain information on either water retention capacities or other morphometrical data on prairie potholes can be found in Haan and Johnson (1967), Kloet (1971), Best (1978), Best and Moore (1979), Hubbard (1982a), and Hubbard and Linder (1986). Use of the data contained in these reports to estimate water storage capacities of pothole basins on any particular site should be done with caution; Hubbard (1982a) found that use of predictive equations to estimate water storage volume based on surface area of potholes (e.g., Hann and Johnson 1967; Best 1978) could lead to extremely erroneous figures.

SUMMARY

Prairie potholes are focal points in the hydrological regime of the glaciated prairie. They are sites where runoff water collects and is temporarily stored allowing it to be either evapotranspired or to seep into the groundwater. Groundwater recharge wetlands are typically either temporary-wetland-dominated or seasonal-wetland-dominated basins, have very low conductivities, and have noncalcareous and nonsaline soils in the central portion of the depression. The central soils of recharge wetlands typically have very deep sola, with a morphology and chemistry indicating a consistent downward water flow, such as the presence of eluvial horizons or argillic horizons. Due to upward-moving groundwater, discharge wetlands have the least developed sola and are calcareous and saline. They are usually semipermanent-wetland-dominated, intermittently-exposed-wetland-dominated, permanent-wetland-dominated, intermittently-flooded-(hypersaline)-wetland-dominated, and saturated-wetland-dominated basins. Flowthrough wetlands are intermediate in salinity between recharge and discharge wetlands and are calcareous. Flowthrough wetlands are typically semipermanent-wetland-dominated and intermittently-exposed-wetland-dominated basins, but probably also include some seasonal-wetland-dominated and permanent-wetland-dominated basins. Although a pothole may at times change functions due to water table fluctuations, the soil should indicate the average long-term flow patterns.

The watersheds in the PPR are typically nonintegrated, most runoff being stored in depressions. When potholes overflow, the effective drainage area of the terminal receiving waters expands, allowing runoff from a larger drainage area to cause flooding. Floods are natural recurring events. However, if these depressions are drained, their small watersheds become a permanent part of the larger watershed's contributing area, thereby increasing the potential for more frequent flooding. The evidence for this is overwhelming, but to date, no one has experimentally verified it.

No valuation data are available for the hydrological functions of wetlands. Thus, a dollar figure cannot be attached to wetlands in the PPR for their groundwater recharge or water retention functions. Their value for groundwater recharge may prove to be phenomenal, as evidence exists to show that the water stored in the till may be an important source of soil moisture recharge. This function needs to be investigated for its importance to the agricultural productivity of this drought-prone area. In addition, the artificial drainage of groundwater discharge and flowthrough wetlands may lead to soil salination at the site--a process that could not only render the site useless for the production of agricultural crops, but also most native plant species.

PRAIRIE POTHOLES AS NUTRIENT SINKS

Wetlands have been purported to act as nutrient (N and P) sinks for inflowing waters and have even been used in tertiary wastewater treatment (Kadlec 1979b; Wile et al. 1981). In the PPR, only one study has been conducted on nutrient sink functions of a large semipermanent-wetland-dominated basin in Iowa (Davis et al. 1981).

Davis et al. (1981) studied water quality in a 365-ha semipermanent-wetland-dominated basin with a 2562-ha watershed in north-central Iowa. Land use in the basin was primarily row-crop agriculture (corn and soybeans). They measured nitrogen and phosphorous levels in the influent and effluent throughout an entire drawdown-refill cycle. During the drought years (3 out of the 4 years studied), there was no effluent, and the marsh served as a sink for N, P, and soluble organic C. During a wet year, when influent and effluent were "normal," the greatest impact of the marshes was on inorganic N, particularly NO_3-N. The marsh removed 86% of NO_3-N entering the marsh. Of the inorganic N entering the marsh, 96% was NO_3-N. In regard to NH_4-N, the marsh removed 78% of the amount entering in precipitation and runoff. When one considers that additional (autogenic) NH_4-N was generated in the marsh by decomposition, the reduction was impressive. Levels of Kjeldahl-N and organic forms of P in the marsh water were not affected appreciably as this water flowed through the marsh. Outputs of soluble organic C exceeded inputs by 71%. They concluded that use of prairie glacial marshes to treat agricultural drainage water can be of most benefit in removing nitrogen.

The marsh studied by Davis et al. (1981) was atypical of many prairie potholes in that it had an outlet for surface water flow. Most potholes only occasionally, if ever, overflow. Thus, any nutrients in runoff waters are retained in the wetland, with the only avenues for leaving being by seepage to groundwater, gaseous loss to the atmosphere, or by animal export. Traditionally, animal export of nutrients has been considered minor but remains poorly studied (Kadlec 1979a). Seepage to groundwater has likewise not been studied in PPR wetlands. For P, it would seem that seepage to groundwater would be minimal. For even though P may become more available to plants during soil inundation accompanied by a decrease in redox potential (Mohanty and Dash 1982; Ponnamperuma 1984), its movement out of the wetland via groundwater is likely to be negligible due to the affinity of P for clay minerals at alkaline pH values. Most prairie wetland soils and the underlying tills are both high in clay and alkaline. Nitrogen species are affected by microbial transformations that are governed by redox. Nitrate, being very soluble at any redox potential, may possibly move out of the bottom of wetlands to groundwater; however, to do this, it must escape past the root zone of the hydrophytes, plus the actions of denitrifying bacteria. This has not been studied in PPR wetlands. But the very slow seepage outflow rates for typical seasonal-wetland-dominated and semipermanent-wetland-dominated potholes, 0.0008 to 0.0088 foot per day (0.24 to 2.7 mm per day) (Shjeflo 1968), make escape of NO_3-N to groundwater seem unlikely. However, Sloan (1970) reported a seepage outflow rate in an Ephemeral Pond (i.e., Class I of Stewart and Kantrud system; nonwetland by the Cowardin system) of 0.5 foot per day (152.4 mm per day). It may be that rates as fast as that may allow for NO_3^- escape to groundwater--especially when it is considered that Ephemeral wetlands typically hold water only in the very early spring before vascular plant activity becomes high. It would seem that the most probable time for NO_3^- to escape to groundwater in temporary-wetland-dominated and seasonal-wetland-dominated potholes would also be in the very early spring.

Although NO_3-N may seem unlikely to move (to an appreciable extent) to groundwater, NH_4-N would seem to be a likely candidate. Ammonium (NH_4^+) is the first inorganic N compound to be released during decomposition of organic matter. It builds up in anaerobic soils due to lack of conversion to NO_3^- by aerobic bacteria (Mohanty and Dash 1982; Ponnamperuma 1984). Like NO_3^-, NH_4^+ can also be taken up by plants as a source of N (Mengel and Kirkby 1982). NH_4^+ is regarded as the only source of N available to plants in continuously waterlogged soils (Patrick and Mahapatra 1968). Therefore, if NH_4^+ is to seep to the groundwater, it must make it past the root zone. When roots are not actively taking up N (such as may occur during the early or late part of the growing season), it is conceivable that those pothole wetlands that are groundwater recharge types may pass N to the groundwater. However, NH_4^+ may be chemically fixed in the lattice of clay minerals or adsorbed on soil colloids, processes that are favored by a high content of 2:1-type clays (e.g., smectites), alkaline pH, and alternate wetting and drying cycles (Ponnamperuma 1984). All three of these conditions are typical in prairie potholes. Additionally, NH_4^+ may diffuse to the aerobic-anaerobic interface where it can be nitrified to NO_3^- on the aerobic side and subsequently be denitrified and lost (N_2 or N-oxides) from the system on the anaerobic side (Mohanty and Dash 1982; Ponnamperuma 1984). Alternate wetting and drying cycles favor denitrification (Reddy and Patrick 1975).

Due to the lack of research on nutrient movements in prairie wetlands, the nutrient sink functions of these systems can only be speculated upon. However, the conditions in prairie wetlands would indicate that potholes probably act as nutrient sinks, for both P (merely by simple detention) and N (by immobilization or gaseous loss). When potholes are drained, however, any nutrient sink functions that potholes may have may be lost. Jones et al. (1976), using regression analyses, investigated the relationship between land use and nutrient output in 34 watersheds in northwestern Iowa. They found that livestock were an identifiable source of P and NH_3-N (=NH_4-N) within the studied watersheds. They also found that NO_3-N was negatively related to the percentage of area in wetland. Wetlands likely reduced NO_3-N because they are areas of anaerobic decomposition, resulting in denitrification and a gaseous loss of N_2. Although P and N could not be identified with the percentage of the watershed in row crops, grassland, or urban areas, sampling of specific watersheds indicated high P, NO_3-N, and NH_3-N in runoff from those areas. Specific sources of the high background nutrient levels in the study could not be identified.

Sulfur is perhaps the most abundant nutrient (albeit a secondary nutrient) in prairie wetlands. With the exception of strictly groundwater recharge wetlands situated at high local elevations, sulfate (SO_4^-) is either the dominant or codominant anion in prairie wetlands (Rozkowski 1969; Sloan 1972; Stewart and Kantrud 1972; Arndt and Richardson 1986; LaBaugh et al. 1987). Sulfate, like nitrate, is subject to reduction by microorganisms. Biochemical reduction of SO_4^- to H_2S requires organic matter as a source of energy. The H_2S produced can leave the system (to the atmosphere) or dissociate to be either further reduced to FeS in the anoxic zone or reoxidized back to SO_4^- in the oxic zone. Gaseous loss of S represents a permanent sink, while reduction to FeS represents a temporary sink. The utilization of organic matter during biochemical reductions may be an important contributing factor in the maintenance of mineral wetland soils in prairie potholes.

Sediment entrapment is another aspect of pollution control that pothole wetlands may provide to society. The nature of pothole wetland soils is to accumulate sediments that wash into the depression with runoff water (Richardson and Bigler 1984). Although Martin and Hartman (1987) found that pothole basins with cultivated watersheds accumulated sediments at a rate about two times that of basins with grassland watersheds, documentation of increased siltation rates in waters receiving the discharges of artificially drained wetlands in this region has not been done.

SUMMARY

The nutrient sink functions of prairie pothole wetlands are the least studied of all pothole functions. Based on studies conducted outside of the PPR, it would seem that prairie pothole wetlands should function as sinks for N, P, and S. Much of the N and S is probably sent to the atmosphere. P, however, is probably stored in the sediments. More work is needed to ascertain the effect that artificial drainage of wetlands has on the nutrient pollution, as well as sediment pollution, of waters receiving wetland drainage into them. As little scientific work has been done, economic valuation studies have likewise not been done.

WETLAND VEGETATION

Wetland vegetation (i.e., species composition, productivity) is a function of the wetland environment. In addition to playing roles in the hydrological and chemical regimes of wetlands, the vegetation functions by providing energy, nutrients, and spatial habitat to animals. The functioning of vegetation in the hydrological and chemical regime has already been discussed. The support of native secondary production will be referred to in later sections of this report. In this section, a more direct function of wetland vegetation will be discussed--the use of pothole vegetation as forage for domestic livestock. But in preface to that, a brief overview of the role of disturbance in prairie pothole plant ecology will be given. Disturbance, or the lack of it, is continually affecting species composition of wetland plant communities and therefore affects classification and delineation as well as the wetland's functional significance for livestock forage and wildlife habitat.

DISTURBANCE AND PRAIRIE WETLANDS

The early work on classifying prairie potholes by vegetation has been briefly summarized in Stewart and Kantrud (1971, 1972) and Millar (1976), who concluded that salinity and water permanence (i.e., water regime) are factors that influence the vegetation. In a series of studies using multivariate techniques to discern relationships between vegetation and environmental factors in prairie wetlands, Walker and Coupland (1968, 1970) and Walker and Wehrhahn (1971) also found that salinity, water regime, and disturbance were the main factors controlling species composition.

The classification systems of Stewart and Kantrud (1971), Millar (1976), and Cowardin et al. (1979) all recognize and use the influence of water permanence and salinity on vegetation in their schemes. The two regional systems provide species lists of indicator plants for the various water regimes and salinity categories. The effects of disturbance, either natural or man-induced, including those of prolonged drought or prolonged ponding are also considered by both systems. Under extreme hydrological conditions, wetlands that normally exhibit species characteristic of a certain water regime may develop species characteristic of another regime.

A large number of studies have investigated and discussed the effects of land use and changing water regime on species composition of prairie wetlands (e.g., Weller and Spatcher 1965; Walker and Coupland 1968; 1970, Walker and Wehrhahn 1971; Stewart and Kantrud 1971, 1972; Millar 1973, 1976; van der Valk and Davis 1976a,b, 1980; van der Valk 1986). Useful reviews have been compiled by Fulton et al. (1986), Kantrud (1986), and Hubbard et al. (1988). Although species composition of a wetland stand is dependent on the contemporary water regime and other disturbances, it is also dependent on past disturbances and the present seed bank. Seed bank studies of prairie wetlands have been conducted by van der Valk and Davis (1976b, 1978). Based on Gleasonian successional theory, van der Valk (1981, 1982) has developed a conceptual model that uses life history aspects of adult and seed bank species to predict species compositional changes in prairie wetlands due to disturbance.

The above cited studies will not be reviewed here, but it is of the utmost importance that most of these studies be thoroughly digested by potential prairie pothole biologists, as well as other scientists that may have to deal with these wetlands. Most prairie pothole wetlands are chronically disturbed, especially when it may be considered that normal water level fluctuation is actually a form of natural disturbance. However, common gross disturbances have been categorized by Stewart and Kantrud (1971, 1972) and need to be presented here in order for the reader to appreciate the prairie pothole situation. The disturbance situations described here are (1) natural drawdown--soil exposing events due to drawdown on uncultivated soils, (2) cropland drawdown--soil exposed after drawdown that had been tilled prior to reflooding, and (3) cropland tillage--tilled wetlands that are left fallow and remain dry. Ubiquitous weedy annual and biennial forbs and grasses, as well as some weedy perennials, frequently colonize in these situations. Many emergent species also germinate during drawdown (Kadlec 1962; Harris and Marshall 1963; Meeks 1969; van der Valk and Davis 1978). Soil-exposing events, caused by natural drawdown, are more common among semipermanent wetlands where open water areas become exposed. However, prolonged ponding in seasonal wetland can also result in emergent species death and conversion to open water (an excellent discussion of this is found in Millar 1973), after which drawdown exposes the bare soil. However, if litter accumulation is excessive, then bare soil may not be exposed, resulting in no germination until the litter has broken down (van der Valk 1986); many emergent species' seeds germinate best in light (Galinato and van der Valk 1986). The cropland drawdown and cropland tillage categories are most common among temporary-wetland-dominated and seasonal-wetland-dominated basins. However, the cropland tillage category only occurs among seasonal-wetland-dominated basins during years of prolonged drought. The communities in the cropland tillage category, regardless of the kind of wetland, are typically composed of the ubiquitous weedy species; obligate hydrophytic species typically do not germinate unless the substrate becomes saturated.

Natural disturbance in the form of drawdowns, due to the unstable climatic conditions of the prairie, has been deemed a necessary part of the "marsh cycle" of semipermanent-wetland-dominated prairie potholes (Weller and Spatcher 1965; Weller 1981). A typical cycle begins with a wetland at drawdown when mud flat annual species and emergent hydrophyte seeds germinate. Increasing water levels over the ensuing years kills the mud flat annuals and allows full emergent development. After several years of high water, emergent vegetation gives way, either due to muskrat (Ondatra zibethicus) herbivory or unfavorable soil conditions, and the marsh becomes open water. Drought causes declining water levels until another drawdown develops. During drawdown, accumulated organic matter decomposes, releasing nutrients back into the system, and plant species germinate. The cyclic nature of the climatic regime of the prairie controls this cycle, and aberrations in climatic patterns can cause resultant aberrations in the wetland cycle.

PRODUCTION AND QUALITY OF WETLAND VEGETATION

Fulton et al. (1986) have summarized the results of 16 investigations of prairie pothole wetland standing crops. Table 2 was taken from that publication and lists the typical yields expected at three times during the growing season in stands of varying species composition within three common water regimes. These data show a trend of increasing production from temporary to semipermanent wetland. However, this is not a strict trend. Hubbard (1988) found that in one of two seasonal-wetland-dominated basins (Carex atherodes dominated) that had experienced prolonged ponding for 2 years, the peripheral temporary wetland standing crop was higher than that of the emergent seasonal wetland. The prolonged ponding caused death of emergents (as may have been predicted based on Millar 1973) in the center of the pond creating open water in one and sparse emergent growth in the other. The emergent seasonal wetland (situated peripheral to the central open zone, but interior to the temporary wetland) was probably also impacted (thinned) by the prolonged ponding. Thus, depending on perturbations, the trend of increasing production from temporary to semipermanent wetland may not always hold. It is important to keep in mind that in this discussion only emergent plant standing crops are being considered; total net primary production (which may include algae and submersed vascular hydrophytes) trends may be different.

The standing crops of prairie wetland vegetation are generally high. In relation to native mixed grass prairie uplands, season-long means of wetland standing crops were up to twice as high as upland standing crops in two seasonal-wetland-dominated potholes dominated by Carex atherodes in eastern South Dakota (Hubbard 1988). Cosby (1964) also found that in a seasonal-wetland-dominated basin dominated by Scolochloa festucacea in mixed prairie in North Dakota, the yields could be over twice as high as those on the adjacent uplands. At a site just to the east of the PPR in Minnesota, Bernard (1974) also found that a stand of Carex rostrata was more productive than the adjacent upland dominated by Poa pratensis. While the yields of native wetland vegetation may be typically higher than those of native uplands, they are not always higher than domesticated and cultivated upland forages (e.g., see data in Heath et al. 1973; Ross and Krueger 1976).

In South Dakota, Hubbard (1988) found that late-season standing crops in six stands of seasonal wetland vegetation ranged from 823 to 1229 g/m^2 (3.7 to 5.5 tons/acre). Yields of Bromus inermis (the most common cool-season forage grass in the State) from a nearby locality at comparable dates ranged from 466 to 731 g/m^2 (2.1 to 3.3 tons/acre) (Ross and Krueger 1976). However, Ross and Krueger (1976) report yields of from 583 to 928 g/m^2 (2.6 to 4.1 tons/acre) at comparable dates for Panicum virgatum (a domesticated native warm-season

Table 2. Typical yields (tons/acre), summarized from 16 studies, of common species from the major water regimes of prairie potholes (modified slightly, from Fulton et al. 1986).

Water regime and species	Early June	Mid-July to Mid-August	Early September
Temporarily flooded	**1**	**2**	**1**
Calamagrostis inexpansa-Carex praegracilis-C. lanuginosa-C. laeviconica	3/4	2	1 1/2
Spartina pectinata	3/4	2	1 1/2
Hordeum jubatum-Distichlis stricta	1/4	1	3/4
Seasonally flooded	**1 1/2**	**3 1/2**	**2**
Sparganium eurycarpum	3/4	2 1/4	1 1/4
Carex atherodes	1 1/2	3 1/2	2 1/2
Polygonum coccineum	1/2	3	2 1/4
Scolochloa festucacea	1	3 1/2	2 1/2
Carex atherodes-Polygonum coccineum-Scolochloa festucacea	1 1/2	3 1/4	2 1/2
Beckmannia syzigachne-Glyceria grandis-Eleocharis palustris-Alisma plantago-aquatica-Sagittaria cuneata	1/2	1 1/2	3/4
Eleocharis palustris	1/2	1 1/2	1/2
Scirpus americanus	—	2 1/2	—
Semipermanently flooded	**1 1/2**	**4 1/2**	**3**
Scirpus heterochaetus	—	3 1/2	—
Scirpus validus	—	2 1/2	—
Scirpus fluviatilis	1/4	3	1
Typha latifolia	3/4	4 1/2	3 1/2
Typha glauca	2	6 1/2	6
Scirpus acutus	—	4	—
Scirpus maritimus	—	1	—

species). Thus, while yields of Bromus inermis were all lower than the seasonal wetland yields, the higher yields of Panicum virgatum are comparable.

General statements about the nutritional quality of prairie pothole vegetation are difficult to make. Proximate analytical data on 32 species that are found in the PPR were compiled from a number of studies (not all of which were conducted in the PPR) and have been listed in Linder and Hubbard (1982) and Fulton et al. (1986). Hubbard (1988) reported nutritional quality data on mid-summer collections of 27 species of temporary and seasonal wetland species, 18 of which were not previously reported in the above compilations. These data show that there is a large amount of variability in the quality of the various species. They also show that species characteristic of semipermanent wetland are generally very poor forages in comparison to the group of species characteristic of temporary or seasonal wetlands. However, for those species that have data listed for more than one date, the general trend in quality is similar to that of upland species; the earlier in the season the better the quality. Caution must be used when considering these data to be representative of a species' nutritional quality. Forage quality can vary within a species due to ecotypic differences, climate or local weather, phenological stage, and site fertility, or whether or not the plants are from a first cutting or an aftermath cutting.

The most complete data sets (that were actually collected in the PPR) of seasonal wetland species exist for whitetop (Scolochloa festucacea) (Smith 1973; Neckles 1984; Hubbard 1988), slough sedge (Carex atherodes) (Johnston and Bezeau 1962; Corns 1974; Hubbard 1988), and burreed (Sparganium eurycarpum) (Hubbard 1988). For temporary wetland species, the most complete data exist for northern bluejoint (Calamagrostis inexpansa = C. stricta according to Great Plains Flora Association 1986) (Johnston and Bezeau 1962). For semipermanent wetland species, season-long data exist for this region only for hybrid cattail (Typha x glauca) (Hubbard et al. 1987). For all of the above reported species, crude protein values are highest prior to flowering and are adequate for many classes of beef cattle (National Reasearch Council 1984). Digestibilities and crude protein content of these species are more comparable to native wild species and domesticated (tame) grasses than they are to alfalfa (Medicago spp.). However, in a study of entire plant communities (i.e., entire clip plots were analyzed rather than individual species), Hubbard (1988) found that while yields were significantly higher in the peripheral temporary and central seasonal wetland of two seasonal-wetland-dominated potholes as compared to the upland prairie, digestibilities (in vitro) were significantly lower for the wetland vegetation than the upland vegetation. Crude protein content comparisons, however, were not consistent.

In all cases studied, peak nutritional quality for seasonal wetland species occurs prior to peak standing crop in early to mid-summer (Smith 1973; Neckles 1984; Hubbard 1988). Thus, peak quality may often occur prior to drawdown. Therefore, to harvest seasonal wetland species for hay of optimum quality, they should be cut as soon as possible after drawdown in early summer. When the soil is wet, grazing is the most efficient means of forage utilization. However, grazing of wetlands should be closely monitored, as cattle may have negative impacts on the rhizomes of wetland species. Hooves sink deeply into the soft wet soil. Management recommendations are given by Smith (1973) and Neckles et al. (1985) for whitetop, and by Hubbard (1988) for whitetop, slough sedge, and burreed.

Valuation studies for wetland forage in the PPR could not be found. Indeed, considering the variety of species that can be found within and among the various water regimes, the seasonality of nutritional quality, and the influence of disturbance that can effect changes in the entire plant community composition, it is not surprising that valuation data do not exist. From the data reported in the literature cited in this section, hay made from temporary or seasonal wetland vegetation can span the range from a Grade 2 grass hay to Sample Grade (graded according to Rohweder et al. 1981), depending on species and time of cutting. The former is about good enough as a sole source of feed for lactating cattle, while the latter needs supplementation, even as a maintenance ration for mature bulls (see National Research Council 1978, 1984). This variable range in quality is about the same as one would expect from native upland vegetation in the northern prairies (e.g., Clarke and Tisdale 1945; Moxon et al. 1951.; Embry et al. 1956; Johnston and Bezeau 1962; National Research Council 1982). Thus, one might consider potholes to be about equal in value to native prairie uplands; the slightly lower digestibilities found by Hubbard (1988) may be more than compensated for by the larger standing crops in the wetlands.

Temporary-wetland-dominated basins should yield a harvestable hay crop in all years, and seasonal-wetland-dominated basins should yield a hay crop in most years. In years of above "normal" runoff, seasonal-wetland-dominated basins may contain water throughout most of the growing season resulting in a situation where grazing may be the only means by which to harvest the forage. In most years, the peripheral temporary and seasonal wetlands of semipermanent-wetland-dominated basins can be either mowed or grazed; the central semipermanent wetland can usually be grazed but, with the exception of *Typha* spp., are seldom used by livestock for grazing. However, during drawdown, the central portion of semipermanent-wetland-dominated basins can develop seasonal wetland species; in which case it can be used like any other stand of seasonal wetland species.

SUMMARY

The plant communities of prairie potholes are dynamic; responding essentially to disturbance (both natural and maninduced) and salinity. The most prevalent natural disturbance is water level fluctuation. These disturbances can cause shifts in plant species composition from year to year. The forage value of the many species that occur in potholes is variable, making general statements difficult to make. However, wetland species appear to be less digestible, on average, than upland species. Nonetheless, if harvested at the right time, species such as whitetop and slough sedge make adequate hay. No economic valuation studies exist for wetland forage in the PPR. However, on a local basis, the average per ton price for upland native prairie hay, or average per acre grazing fee (realizing that wetlands may be up to two times, or more, productive than native uplands) may be realistic to use for wetland forage.

WETLAND FAUNA

Prairie pothole wetlands provide a diversity of animal species with a place to live. Many of these species are of economic importance (e.g., waterfowl, muskrats, mink, pheasants, deer), while other species provide links in the food chain (e.g., invertebrates which are used as food by waterfowl) to species of economic importance or are important for ecological, scientific, or aesthetic reasons (e.g., nongame birds). Published studies on the habitat requisites of many pothole wetland species are scarce. However, the body of literature on waterfowl in prairie pothole wetlands is large. In this section, an overview of the animals that use potholes will be provided. In addition, the few studies that have placed a value on pothole wildlife functions will also be reviewed.

WATERFOWL

The importance of the PPR to breeding dabbling ducks (*Anas* spp.) cannot be overstated. Bellrose (1979) states that 41% of the North American population of breeding dabbling ducks use this region. A complete and excellent review on the use of prairie wetlands by waterfowl has recently been prepared by Swanson and Duebbert (in press). Much of the material discussed in this section has been condensed from that paper. For more detail on aspects of prairie waterfowl ecology, the original paper should be consulted.

When the earliest of migrant ducks return to the region in spring (e.g., mallards--*A. platyrhynchos*, and pintails--*A. acuta*) the large semipermanent-wetland-dominated basins are typically still frozen. The first to warm-up and hence, thaw, are the small wetlands: temporary-wetland-dominated and seasonal-wetland-dominated basins. Class I ponds (classified according to Stewart and Kantrud 1971; nonwetland according to Cowardin et al. 1979) are not frequently used by waterfowl (Stewart and Kantrud 1973; Kantrud and Stewart 1977; Ruwaldt et al. 1979) as they are typically only wet for a few days and are usually dry shortly after the soil thaws. Temporary-wetland-dominated and seasonal-wetland-dominated basins provide space needed by breeding pairs so that interspecific encounters are kept to a minimum (Drewien and Springer 1969). Although the data of Stewart and Kantrud (1973); Kantrud and Stewart (1977), and Ruwaldt et al. (1979) indicate the temporary-wetland-dominated basins were used by less than 10% of the breeding pairs of most species, Ruwaldt et al. (1979) did find that in 1 of the 2 years censused about 12% of the northern shoveller (*A. crecca*) pairs observed were on these basins. When expessed on a density basis (breeding pairs/unit of surface area), temporary-wetland-dominated basins frequently recieve higher duck use than other wetlands by some species of dabbling ducks (Stewart and Kantrud 1977; Ruwaldt et al. 1979). It should be pointed out that many potholes could be dry at the time of census causing a misrepresentation of duck preference for a certain kind of wetland basin if they are forced to use other kinds. In addition, the method used to express the results can bias conclusions about the importance of the basin kinds (see discussion in Swanson and Duebbert, in press). Nonetheless, the data of Evans and Black (1956), Drewien and Springer (1969), Stewart and Kantrud (1973), Krapu (1974), Swanson et al. (1974), Kantrud and Stewart (1977), and Ruwaldt et al. (1979), among others (see Swanson and Duebbert, in press), indicate an overwhelming preference for seasonal-wetland-dominated basins by dabbling ducks.

Aside from pair isolation, seasonal-wetland-dominated basins provide a source of protein-rich invertebrate foods for breeding hens. Reviews of the invertebrate foods of pothole breeding ducks have been published by Swanson et al. (1979) and Swanson and Duebbert (in press). Krapu (1979, 1981) and Swanson et al. (1986) have demonstrated the physiological importance of diets high in invertebrates to nesting hens. The high use of seasonal-wetland-dominated basins is attributed to the faster rate of warming in the spring (as opposed to semipermanent-wetland-dominated basins), thereby causing invertebrates to be more readily available. Dwyer et al. (1979) found that nesting mallard hens preferred temporary-wetland-dominated and seasonal-wetland-dominated basins, and that individual hens used from 7 to 22 different basins (of all water regimes) in a season.

Semipermanent-wetland-dominated basins are also used extensively by breeding pairs of dabbling ducks, but their use by diving ducks (Aythya spp.) is especially high (Stewart and Kantrud 1973; Kantrud and Stewart 1977; Ruwaldt et al. 1979). Breeding female diving ducks, like the dabblers, also consume high amounts of invertebrates during the breeding season (Bartonek and Hickey 1969; Swanson and Meyer 1973) the invertebrates being obtained from the semipermanent-dominated-wetland basins. The later invertebrate availability, as compared to temporary and seasonal wetland, in semipermanent wetland coincides with the later breeding dates of the diving ducks. The peripheral seasonal wetlands in these basins are used by waterfowl in the same manner as they are in seasonal-wetland-dominated basins. The dabbling ducks using seasonal wetland habitats, regardless of the kind of basin, switch to more use of semipermanent wetlands as the seasonal wetlands drawdown.

Juvenile waterfowl also require invertebrate protein sources both dabbling ducks (Sugden 1973; Swanson 1985) and diving ducks (Bartonek and Hickey 1969; Sugden 1973). If broods hatch early, seasonal-wetland-dominated basins are preferentially used by mallard broods when available (Talent et al. 1982). When seasonal-wetland-dominated basins drawdown, hens move their broods to semipermanent-wetland-dominated basins. Talent et al. (1982) found that as many as 10 different basins were used by individual mallard broods, hence stressing the importance of the "wetland complex." They also found that hens were selecting for ponds containing high numbers of chironomid larvae for brood-rearing sites. The data presented by Duebbert and Frank (1984) also demonstrate the importance of seasonal-wetland-dominated and semipermanent-wetland-dominated basins to broods. In that study, data collected from 1958 to 1978 (exclusive of 4 years) show that 82% of the broods observed were on these two kinds of basins--these kinds of basins composing only 54% of the wetland area.

A "wetland complex" is an area that contains many basins in close proximity to one another. A good complex should have one or more semipermanent-wetland-dominated basins to provide "guaranteed" brood-rearing habitat, and several temporary-wetland-dominated and seasonal-wetland-dominated basins for breeding-pair space and feeding habitat, and for brood habitat if water conditions permit. During dry years, when only the semipermanent-wetland-dominated basins are ponded, the duck production that occurs should provide for a source of returning birds to the area in the following year. When water conditions are good and temporary-wetland-dominated and seasonal-wetland-dominated basins are ponded, the number of ponds allows for not only homing hens and their mates to use the area, but also provides the space needed to accommodate pioneering birds, and overall production should be increased. Bellrose (1979) provides an analysis of mallard breeding numbers versus young produced in the PPR at seven levels of abundance of wet ponds in May. The analysis is striking; the more ponds, the more young produced. This further demonstrates the importance of temporary-wetland-dominated and seasonal-wetland-dominated basins to waterfowl production, as they are the greatest source of year-to-year variability in the number of wet ponds in spring. Very large semipermanent-wetland-dominated basins that have extensive peripheral temporary and seasonal wetlands may provide a similar kind of habitat as a good pothole complex, but may not be able to provide as much space for conspecific breeding pair isolation as the same collective area of smaller wetland basins due to behavioral spacing mechanisms.

To quantify the functional significance of prairie wetlands to waterfowl would be a formidable task. Not only do these wetlands provide breeding habitat for pairs and broods, but also they provide molting habitat for post-breeding adults, staging habitat in the post-breeding but pre-migratory period, and migrational habitat in the spring and fall (Swanson and Duebbert, in press). As nonbreeding waterfowl habitats, prairie wetlands need much more research before these functions can be even crudely quantified (Swanson and Duebbert, in press). But even as breeding habitats, quantification will not be easy. Many studies have provided estimates of breeding pair densities on prairie wetlands of all kinds (e.g., Evans and Black 1956; Drewien and Springer 1969; Smith 1971; Stoudt 1971; Stewart and Kantrud 1973; Kantrud and Stewart 1977; Ruwaldt et al. 1979) but these data will only indicate use or, at best, habitat preferences. Even if these data can be valuated (by some creative assumptions), it would only be a partial measure of the value of waterfowl breeding habitat. The number of young fledged, or some other measure of production, would provide a basis for a better measure of the value of the wetland habitat.

For many waterfowl species (especially dabblers), the use of a wetland by breeding adults and the wetland's productivity of ducklings are influenced by the quality and quantity of nesting cover on the surrounding uplands. The upland habitat not only attracts nesting hens to an area, but also influences predation. Predation on hens, eggs, and young is a very serious problem in the PPR (Cowardin et al. 1983, 1985; Sargeant et al. 1984). Therefore, even if quantified production data (i.e., young fledged per ha of a given kind of wetland) existed, it would have to be considered minimal since most wetlands are probably not producing ducklings at maximal rates due to predation.

RESIDENT GAME SPECIES

Pothole wetlands are important as wintering cover for pheasants (Phasianus colchicus) (Sather-Blair and Linder 1980) and for white-tailed deer (Odocoileus virginianus) in South Dakota (Sparrow 1966; Kramlich 1985). In North Dakota, Harmoning (1976) reported that white-tailed deer does used wetlands as fawning sites. Heavily vegetated (e.g., Typha spp.) semipermanent-wetland-dominated basins provide the best winter cover for these species. Schneider (1985) found that wind velocities in wetlands during the winter in eastern South Dakota were 95% less than those found in nearby shelterbelts. No work has been done to quantify the relationship between pheasant or deer populations and prairie wetlands.

Semipermanent-wetland-dominated basins are the preferred habitat of muskrat (Ondatra zibethicus), but other wetlands in the PPR are used as well. Although muskrats will eat both above and below ground plant material of many species and will live in many habitat situations (see review by Perry 1982), Typha spp. are their mainstay in terms of both food and cover especially in northern North America (Errington 1963). In addition to an abundant supply of cattail, optimum habitat conditions require that water depths be deep enough in winter to avert a "freeze-out" and persistent enough in the summer to avert a total drawdown (Errington 1963). Since water conditions in the PPR are dynamic, and these rodents have a propensity for destroying their food resources (termed "eat-outs"), muskrat populations are likewise dynamic and subject to "boom and bust" fluctuations. A marsh that may support thousands of muskrats in one year may support few in another year. Thus, it would be difficult to assign a generally applicable "muskrats per hectare" figure for semipermanent wetlands. Estimates found in Errington (1963) are extremely variable. Although long-term pelt harvest information collected by State wildlife resource agencies could be used to estimate a general, collective, wetland-resource fur value, accurate values for a specific wetland site may be difficult to attain. General ranges of values for different wetland kinds within specified regions are probably the best valuation data possible. Compounding the valuation problem is the influence that muskrats have on the habitat conditions for waterfowl and other marsh animals (see review in Weller 1981). By influencing the emergent plant cover to open-water ratio (i.e., the wetland "class" in the hierarchy of the Cowardin system), muskrats can influence the carrying capacities of most other marsh animals. An extremely high muskrat population on a wetland may preclude its use by optimum waterfowl numbers.

Mink (Mustela vison) populations are less well studied than muskrat populations, but also appear to be extremely variable (Errington 1963). Estimates of the value of mink supported by wetlands, as for muskrats, will have to be made from fur harvest data and related to the overall wetland resource. Red fox (Vulpes vulpes) and raccoon (Procyon lotor) derive significant portions of their diets from prey items dependent upon wetlands in the PPR (see Greenwood 1981; Sargeant et al. 1984). Therefore, a yet-to-be-determined portion of the value of these resources can be attributable to wetlands. Valuation of any of these species will also be compounded with waterfowl, muskrat, and other wetland wildlife species due to their interdependency for survival. A review of the studies that have been conducted on mammalian game and fur species that are associated with prairie wetlands will be published by Fritzell (in press). That review contains information that will be helpful in formulating assumptions for valuation estimates.

NONGAME SPECIES

Many nongame species inhabit prairie pothole wetlands. For example, Duebbert (1981) found that on six Waterfowl Production Areas in North Dakota, 32 out of 67 nongame species of birds were dependent primarily on wetland habitats. Wetlands accounted for 30% of the study area hectarage. Of this, 24% of the wetland area was composed of seasonal-wetland-dominated basins, and 75% was semipermanent-wetland-dominated basins. On a single large semipermanent-wetland-dominated basin in North Dakota, Krapu and Duebbert (1974) found 34 species of breeding birds as well as many species of migrants and transients. Other studies of nongame bird use of prairie wetlands have been conducted by Weller and Spatcher (1965), Weller and Fredrickson (1974), Weber et al. (1982), Hubbard (1982b, 1984), and Brady and Giron-Pendleton (1983). Studies of nongame mammals have been reviewed by Fritzell (in press). The value of these wildlife resources will be even more difficult to estimate than that of game species, since nongame values are either interconnected with those of game species (e.g., by functioning as prey) or are esthetic.

Wetlands in the PPR support several aquatic species (minnows, frogs, leeches, salamanders) that, even though they may be considered nongame, are important to the commercial baitfish industry and may also be collected as biological specimens for educational institutions (Warnick 1973; Van Eeckhout 1976; Peterson and Hennagir 1980). The bait industry is quite large and valuable to State economies, but reliable data are difficult to obtain. Most surveys are thought to be very conservative because of inadequate reporting. In fact, Warnick (1973) reported that in his survey of baitfish dealers in South Dakota, the figures collected were totally unreliable. The following figures reflect the relatively high value of wetlands to the bait industry. However, these figures do not estimate the actual value of prairie pothole wetlands to the bait industry since the figures include not only bait harvested from Palustrine wetlands in the PPR of these States, but also Lacustrine habitats and waters from outside the PPR.

The most recent information available from Minnesota illustrates the importance of the largest segment of the industry--baitfish. In 1978, 781,960 liters of fathead minnows (Pimephales promelas) were harvested, of which 63% were harvested from public waters. Private waters were leased for minnow production for about $110/year/pond, regardless of acreage. The retail value of wild fathead minnows amounted to about $12.6 million (Peterson and Hennagir 1980).

Fathead minnows and brook sticklebacks (Culaea inconstans) are the most prevalent fish in semipermanent and intermittently-exposed-wetland-dominated basins in the PPR, and Peterka (in press) has reviewed the biology of these species in prairie wetlands. Production and standing crop data for these species are scarce. Payer (1977) estimated a summer production of 18 kg/ha of fathead minnows in a semipermanent-wetland-dominated basin in eastern South Dakota. Ecological information on other aquatic vertebrates used as bait is also scarce.

Other wetland aquatic species are also harvested for sale. In Minnesota, about 43,452 liters of leeches, worth $2.7 million, were collected in 1978 about 56% of which were harvested from public waters (Peterson and Hennagir 1980). In the following year, 55 tons of leeches, worth $3 million, were harvested (Peterson 1981). About 1,800 dozen frogs, 4,200 dozen salamanders, and 5,000 dozen crawfish per year were also harvested in that State between 1976 and 1979 (Peterson and Hennagir 1980). Between 1965 and 1971 in South Dakota, 5,617 kg of frogs were harvested by from 6 to 25 (depending on year) licensed frog harvesters for an average value of $7,214/year (Warnick 1973).

PRAIRIE WETLAND WILDLIFE VALUATION

Although monetary values of wetland wildlife may be hard to measure directly, measurements of the value of the consumptive and nonconsumptive recreation they support are perhaps a meaningful expression of their worth. In terms of direct return to the landowner, Uhlig (1961) found that in Minnesota many farmers were leasing their wetlands to hunters. He found that, at least at that time, the higher priced leases gave returns to the landowner that were equivalent to cropland on a per acre basis. Wetlands may also be leased to bait dealers.

Thompson (1983) surveyed the recreational use of six public wetlands, located within the most populated portion of South Dakota, over the course of 1 year. In that study, over 10,000 people made about 5,000 trips spending over 63,000 man-hours at the sites. Ninety-three percent of all the people and 98% of the man-hours spent at these sites were for hunting. The low nonconsumptive use of these wetlands is, no doubt, a reflection of the rural nature of South Dakota. In a study of Michigan coastal wetlands (Great Lakes), Raphael and Jaworski (1979) found nonconsumptive recreational values to be higher ($366/ha/year) than for hunting and trapping combined ($177/ha/year). The high population density of Michigan places a high demand on these systems for nonconsumptive recreation. The study by Thompson (1983) may be indicative of low nonconsumptive use rates for most of the PPR, and not just South Dakota. However, one might expect that in the extreme eastern portion of the PPR (Minnesota and Iowa), where not only a higher human population exists but also fewer potholes remain, there might be a much higher nonconsumptive use rate.

In a follow-up to Thompson's (1983) study, Johnson and Linder (1986) surveyed a sample of the resident hunters in South Dakota and determined that direct expenditures by them for wetland related hunting in the State for 1982 was over $24,000,000. They also estimated that the total consumers' surplus (a measure of the benefits received in excess of costs paid, i.e., the amount the hunters perceived to be the value of thier wetland hunting experience) was almost $34,000,000. They estimated that this consumers' surplus was $813 per hectare of wetland (all classes) for the State [discounted at 7.875% and using the estimate by Ruwaldt et al. (1979) of 529,000 ha of wetlands in the State]. In terms of mean hunter-days spent on wetlands in 1983, Johnson (1984) reported that 27% were spent on hunting waterfowl, 47% on upland game, 17% on big game, and 9% on predators. In a North Dakota study, Sorenson (1975) estimated that of the $54.3 million of gross business volume generated by hunter expenditures, 56%, or $30.4 million, was attributed to the existence of wetlands in 1973. Based on a nationwide survey of hunters in 1968, Hammack and Brown (1974) calculated that each bagged mallard was worth $3.29.

SUMMARY

Optimum waterfowl production occurs on wetland complexes in the PPR. It is the abundance of ponds, governed primarily by seasonal-wetland-dominated potholes, that can optimize production. Other game species in the PPR are also dependent on potholes, such as white-tailed deer and pheasants. While a diversity of other wildlife species inhabit PPR wetlands and have their own intrinsic value, they apparently contribute little to the monetary value of these regional wetlands. However, the nonconsumptive use value of these nongame species may need further clarification in parts of the region. Due to interrelationships between predator and prey species in these habitats as well as only partial dependence on wetland habitat for some species, the value of wetlands for fur harvest, bait harvest, and as a recreational hunting resource are probably the most meaningful and most readily attainable values. It appears that the value of prairie pothole wetlands as a recreational resource for hunting is great, but it needs to be calculated for the entire PPR.

FURTHER DISCUSSION OF THE WETLAND COMPLEX IN THE PPR

In the vernacular of waterfowl biologists in the PPR, the term "wetland complex" refers to an assemblage of individual wetland basins in relatively close proximity to each other. In the preceding section, a discussion of the importance of a diversity of wetland kinds and abundance of wetland basins for breeding waterfowl was provided. Unfortunately, Just how many wetland basins are needed ? Of what kind ? and In what densities ? are questions that, at present, cannot be definitively answered. However, the question How far away from the rest of the "wetland complex" can a wetland basin be before it is considered disjunct from the complex? may at least be partially answerable.

Table 3 presents some information on the home range sizes of a few species of ducks. Although Table 3 is not an exhaustive listing, it serves to show that home range size is from less than a quarter-section to about two sections in size. With these home range sizes in mind, one might at first consider a wetland basin as being of little value to waterfowl production if that wetland (1) has a dominant water regime of less than semipermanent and (2) is more than about 5 km (about 3 miles) away from the next closest basin in a wetland complex. The first criterion is justified because temporary-wetland-dominated and seasonal-wetland-dominated basins generally do not hold ponded water long enough through the growing season to be able to support a duck brood to flight stage. Semipermanent-wetland-dominated basins generally do hold ponded water long enough to support a brood to flight stage. Therefore, even if isolated, a semipermanent-wetland-dominated basin generally provides acceptable waterfowl breeding habitat; however, its status would be improved if it were part of a good complex. An isolated semipermanent-wetland-dominated basin may provide excellent waterfowl breeding habitat if it contains large peripheral temporary and seasonal wetlands. The justification for the second criterion is somewhat arbitrary, but considering that Dwyer et al. (1979) recorded maximum home range lengths of 5.1 km for two out of six breeding mallard hens, this distance is probably realistic.

Table 3. Some examples of home range sizes of waterfowl in the Prairie Pothole Region and adjacent areas[a].

Species	Home range size	Source
Blue-winged teal	greater than 100 ha	Dzubin (1955)
Blue-winged teal	mean radius: 0.29 km (11 pairs) range: 0-0.7 km	Evans and Black (1956)
Blue-winged teal	mean: 67.6 ha (14 pairs) range: 29.6-86.0 ha	Drewien (1968)
Gadwall	several hundred acres (as reported)	Duebbert (1966)
Mallard	greater than 280 ha	Dzubin (1955)
Mallard	mean area: 467.8 ha (6 hens) mean maximum length: 4.0 km mean maximum width: 1.7 km	Dwyer et al. (1979)

[a] The study by Dzubin (1955) was conducted in the Aspen Parkland Region of Manitoba.

Isolated wetlands with dominant water regimes of less than semipermanent may be of little value to local breeding waterfowl, but may be used by migrant waterfowl when ponded. In addition, isolated wetlands still provide habitat for other avian species, as well as resident game and nongame species. It may be conjectured that noncultivated, isolated wetlands may be more valuable, on a per unit basis, to resident species as winter cover than those that are part of a good complex. It should be pointed out, however, that a wetland that is cultivated in any given year may not be cultivated in other years, due to wetness.

In terms of hydrologic functions, wetland complexes should provide for better groundwater recharge and better water retention than similar acreages of wetlands in a large, single basin. The study by Millar (1971) demonstrated that small wetlands lost water at a much faster rate than large wetlands due to the effect of marginal evapotranspiration; the rate of water loss varied directly with the length of shoreline per unit of pond surface area. Thus, small wetlands will regenerate their storage capacity and be ready to store the next runoff event much more quickly than large wetlands. Since smaller wetlands are more apt to be temporary-wetland-dominated and seasonal-wetland-dominated than larger wetlands (see data in Evans and Black 1956; Kantrud and Stewart 1977; Cowardin et al. 1981), they are more likely to be groundwater recharge wetlands. The small wetlands in a complex, in addition to improving waterfowl pair habitat and foraging habitat, help keep semipermanent-wetland-dominated basins ponded by keeping local groundwater flow systems actively discharging into them. So, not only do buried outwash aquifers and soil moisture levels benefit from groundwater recharge, but also duck brood habitat does as well.

Quantitatively defining the ideal wetland complex for wildlife or hydrological functions must await further clarification by the research community. At present, data on the composition of local undisturbed complexes should provide a first approximation in any given area. Information on numbers, water regimes, sizes, etc., on a gross statewide and physiographic basis can be found in Stewart and Kantrud (1973) for North Dakota and in Ruwaldt et al. (1979) for South Dakota. Information on local areas in the Dakotas can be found in Evans and Black (1956), Drewien and Springer (1969), Cowardin et al. (1981), Wittmier and Mack (1982), Wittmier (1982, 1984, 1985), and Hubbard and Linder (1986). Data collected on Canadian study areas can be found in Millar (1969), Smith (1971), and Stoudt (1971).

CONCLUSIONS

A great deal of qualitative information is known about the functions of prairie pothole wetlands. Prairie potholes are essentially "windows" to the water table that allow surface water and groundwater to interact. By artificially draining pothole wetlands, water tables may eventually be lowered, possibly leading to soil moisture shortages and the drying-up of surficial and shallowlyburied outwash aquifers. Soil salination may result from the drainage and cultivation of groundwater flowthrough and discharge wetlands. Flood frequencies may be increased by pothole drainage. Quantitative information on these functions is needed, however, in order for them to be economically valuated. It seems possible that, once valuated, the value of the hydrological functions of pothole wetlands could dwarf the combined value of all the other functions of these systems. An abundance of small temporary-wetland-dominated and seasonal-wetland-dominated basins are most valuable in terms of surface water detention and groundwater recharge.

Less is known about nutrient sink and sediment detention functions; qualitative as well as quantitative information is needed. Based on studies of other wetland ecosystems, prairie pothole wetlands probably act as sinks for nitrogen, phosphorous, and sediments with respect to the surficial water regimen. Relationships between nutrients and the groundwater regime, especially nitrogen, need particular attention in future research.

Studies on the production of pothole wetland vegetation are numerous and show that wetland standing crops are generally much greater than native upland prairie standing crops or tame cool-season grasses. Many wetland plant species are nutritionally adequate as beef cattle forage if used at the appropriate time.

Prairie pothole wetlands are habitats for many species of wildlife, both game and nongame, they are most notable as waterfowl habitat. It is the semipermanent wetland that is the backbone of a prairie wetland complex.

However, it is the abundance of temporary and seasonal-wetland-dominated basins, in conjunction with the semipermanent wetlands, that provides for optimal waterfowl production. For furbearers and bait species, direct valuations should be relatively easy to make. The direct valuation of most other prairie wetland species will be difficult due to many species' (including dabbling ducks) interdependency on both wetland and upland habitats, as well as competing values between some species. For the short-term situation at least, the recreation that these species provide will perhaps be the best estimation of their economic value. In the Dakotas, at least, wildlife supported recreation is essentially synonymous with hunting. However, nonconsumptive recreational use of these wetlands does exist and needs to be quantified. Based on the existing valuations for those two States, the hunting recreational value is substantial. However, future valuations of prairie wetland dependent hunting need to include the other PPR States.

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16. Abstract (Limit: 200 words)

This report provides a current synthesis of the functions of prairie pothole wetlands. Functions discussed include hydrology, nutrient/contaminant entrapment, forage for livestock, and wildlife support. When known, the economic value of these functions is also considered. In general, hydrologic and wildlife functions are optimized when whole wetland complexes remain intact. Once valuated, the value of the hydrological functions of pothole wetlands could possibly dwarf the combined value of all other functions of these wetland systems. It is hoped that this review will help provide field personnel of natural resource agencies with the information needed to begin to address the difficult task of adequately assessing the functions of wetlands on a case-by-case basis.

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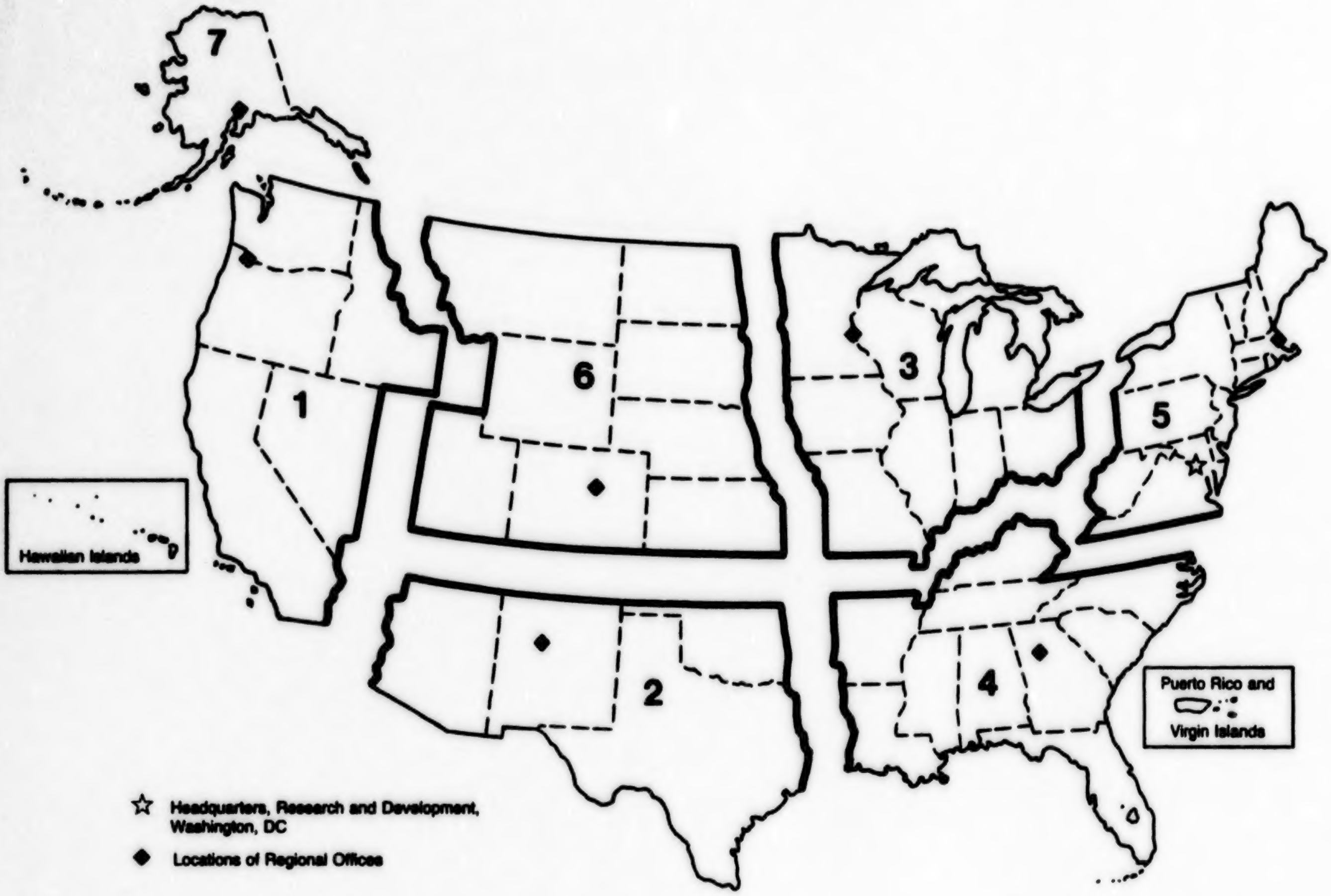
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